XIV. *On the Development and Succession of the Poison-fangs of Snakes.* By CHARLES S. TOMES, *M.A.* *Communicated by* JOHN TOMES, *F.R.S.*

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IN two papers which described the development of the teeth of Batrachia, Sauria, and Ophidia, which were laid before this Society, and appeared last year in the Philosophical Transactions, I gave a brief *résumé* of the literature of the subject, so far as it was then known to me. Between the dates of the reading of my paper and of its appearance in the Philosophical Transactions, Dr. HERTWIG, of Jena*, published a paper on the development of the teeth of Amphibia, in which the figures and the descriptions conform, in most essential particulars, with those accompanying my own paper. Although Dr. HERTWIG does not include in his remarks the groups Sauria and Ophidia, I have gladly taken this opportunity to acknowledge his independent and practically contemporaneous publication of results nearly identical with my own.

As I have so lately summarized the opinions of other observers upon the development of reptilian teeth (*cf.* Phil. Trans. part i., 1875), it will not be necessary for me to recapitulate them again in this paper; but I may be allowed to pass directly to the peculiarities which mark the development of poison-fangs.

At the conclusion of my paper on the development of Ophidian teeth, I remarked that there were noteworthy peculiarities in the formation of poison-fangs, which, for the want of material, I had not been able to make out in all their details. Since that time, by the kindness of my friends Prof. GARROD and Mr. ROBERTSON, of Oxford, I have been enabled to unravel what was before obscure; and the peculiarities of arrangement disclosed will, I venture to hope, be deemed of sufficient interest to justify me in laying them before this Society.

Of poison-fangs Prof. OWEN (Art. "Odontology," 'Encyclopædia Britannica') says:— "In the posterior part of the large mucous sheath of the poison-fang the successors of this tooth are always to be found in different stages of development; the pulp is at first a simple papilla, and when it has sunk into the gum the succeeding portion presents a depression along its inferior surface, as it lies horizontally with its apex directed backwards. The capsule adheres to this inflected surface of the pulp, and the introduction of the duct of the poison-gland is completed by the extension of the borders of the inflected pulp around that tube."

Exception might be taken to several points in this description; but as in my two earlier papers, and in a third, published in the first part of the Philosophical Transactions for

* Archiv f. mikros. Anatomie, Supplementheft 1874 (December).

this year, I have discussed the qualifications which need to be made before we can accept Prof. OWEN'S description of the development of these or any other reptilian teeth, I have simply quoted his words here, as embodying what is commonly known of the development of poison-fangs.

Venomous snakes are divided into two groups—the *venomous colubrine snakes*, in which the poison-fang is attached to a fixed maxillary bone, so that it is always erect, and the *viperine snakes*, in which the maxillary bone carries no other teeth than the poison-fang, and is capable of a rotary motion, by which its fang is erected or laid recumbent (GÜNTHER'S 'Reptiles of British India,' Ray Society, p. 165).

I have had better opportunities of investigating the poison-fangs of the viperine snakes than of the venomous colubrines, of which latter the cobra is the only one which I have been able to procure in a perfectly fresh condition; but, as I shall presently show, there would appear to be well-marked differences in the succession between the two groups*. The relations of poison-fangs to their successors may be most advantageously studied in transverse sections, the specimens having been previously hardened and decalcified in chromic acid.

The appearance presented will vary, according as the section is near to the tip or to the base of the fang. I will commence by the description of a section taken midway in the length of the poison-fang of a rattlesnake (Plate 37. fig. 2).

The figure embraces that which would appear to the naked eye as an elevation when looking into the mouth of the snake—that is to say, the recumbent tooth covered in by its loose fold of mucous membrane (*c* in the figure) and the subjacent region where lie the successional teeth. At the upper part of the figure the poison-fang at present in use (1) is seen lying in a chamber in the mucous membrane, and since it is recumbent and parallel to the long axis of the jaw, it is in transverse section. Beneath it (or, as it would stand in the snake's mouth, above it) are a series of eight teeth of various ages, all seen in transverse section, the oldest lying nearest to the tooth already in use.

The successional teeth are not arranged in a single series, as would be the case in the ordinary serial teeth of the jaws (*cf.* my paper in Phil. Trans. 1875), but in a double row, being obviously placed in pairs.

A more careful inspection of one of these pairs will disclose that although there is no very great difference, yet one of the teeth is a little more advanced than the other. Thus in fig. 2 No. 2 is a little more advanced, both in development and in position, than No. 3, and is the tooth destined to be the next to move into its place and enter upon work. Lower down in the series this difference in point of development is less apparent; indeed the two constituting a pair are generally advanced to about the same stage in their construction.

I have affixed numbers to the several tooth-germs shown in figs. 1 and 2 to indicate

* I have examined several specimens of *Hydrophis* which were preserved in spirit, and believe the arrangement of the successional teeth to be similar to that observed in *Cobra*; but specimens long kept in diluted spirit are ill-suited for such investigations.

the order in which they would succeed to the tooth already in use. It will be seen that the new tooth comes alternately from either side, No. 2 being on the left- and No. 3 on the right-hand side in fig. 2. There is an obvious advantage in such an arrangement, since it insures the least possible loss of time between the shedding-off of one poison-fang and its replacement by another; but if the new tooth passed exactly into the position of its predecessor little or nothing would be gained. Such is not the case, however; there is room upon the surface of the maxillary bone which gives attachment to the poison-tooth for two teeth, side by side (see fig. 4). The tooth actually in use occupies one side, where it is anchylosed by its base, side, and front, whilst its successor is getting ready to take possession of the vacant place by its side. Thus one poison-fang occupies the innermost position possible on the maxillary bone, the next one the outermost, and so they go on alternating. It will at once be obvious that such an arrangement of the successional poison-fangs is admirably adapted for securing a speedy replacement of a lost tooth; and sections taken near to the base of attachment almost invariably (unless it so happens that the attached tooth has only just become fixed and its predecessor but just shed off) show a second tooth (2 in fig. 4) which is in the process of attachment by the rapid development of a coarse bone (*b* in the figure) about its base.

In fig. 2 (1) the tooth in place alone occupies the chamber in the pouch of mucous membrane which covers in the recumbent poison-fangs, all the successional teeth still remaining bedded in the mass of loose connective tissue in the midst of which they are developed.

In fig. 1, however, a different stage in the process is represented; it is taken from a section of the head of an English viper, in which I was so fortunate as to hit upon the moment, so to speak, of the change from an old tooth to a new one. The chamber in the mucous membrane is seen to contain sections of *two* teeth, which are separated from one another by a flap of connective tissue (*b*). This flap of connective tissue, visible also in fig. 2, is continuous with the slightly specialized connective tissue which lies between and separates the two series of successional teeth; and an apparent use for it is very obvious, though only actual observation can determine whether it has any other. It would seem probable that it serves to keep the advancing tooth to its own side, as it would be almost impossible for a tooth of the one series to get round it and so become wrongly placed on the side appropriated to the other series; it would also serve, by limiting the space in which the advancing tooth lies, to keep it straight—that is to say, to prevent it from diverging to the one side or the other in its own length.

In fig. 1 the tooth already used (1) is about to be cast off, and its successor (2) has already passed out of the region where teeth are being developed, and is doubtless becoming rapidly attached. In fact fig. 4 is a section from the very same specimen, though, unfortunately for the comparison, the section has been mounted with the other surface uppermost, so that the sides are transposed. However, 2 on the left of fig. 4 is the very same tooth as 2 on the right of fig. 1, the first-named section being taken close

to its base, by which it will be anchylosed to the maxillary bone, this process being in fact already commenced *.

The development of poison-fangs in two parallel series, the teeth being arranged in pairs of almost equal ages, would suggest that the succession is very rapid and quite regular; were it not so, one would expect to find that the teeth of one series would be very markedly in advance of their fellows in the parallel series, which is not the case. Moreover the large number of successional teeth (ten) is unusual. I know of but one other place where more than three teeth can be found in preparation to succeed a single tooth, and that place is in the jaws of Ophidia, where six or seven of the ordinary serial teeth, in different stages, may sometimes be seen.

I believe that the development of poison-fangs in two parallel series would be found to be the rule, if indeed it be not universal, in viperine poisonous snakes. I can only positively answer for the English viper, the puff-adder, and the rattlesnake, these being the only poisonous snakes of this group which I have obtained quite fresh. But, judging from the vacant spaces by the side of the attached poison-fangs in macerated skulls, the arrangement holds good in all viperine snakes that I have seen.

The region where teeth are being developed in a *colubrine* venomous snake, the Indian cobra, is strikingly different. There is no double series, but the successional teeth are disposed in a single series, just like the teeth of a harmless snake, or the mandibular or pterygoid teeth of a poisonous snake. In fact the description which I gave in a former paper of the manner in which the teeth of the harmless Ophidia are developed would apply strictly to the poison-fangs of a cobra, save only that the individual tooth-germs are modified to form canaliculated teeth.

In fig. 5 there is seen a line of inflected epithelium (g) running in from the oral epithelium (a); this, which goes to form the enamel-organs of successive germs, is lost sight of behind the first successional tooth-germ ($_2$); its free extremity, already slightly dilated near where it will form a fresh enamel-organ, is seen at f. The section, having been taken a little behind the erect poison-fang already in use, shows no trace of this; but sections including the working tooth do not in the cobra show much of its successors, which lie behind it and are recumbent, whilst it is erect. The new tooth occupies more nearly the same spot as its predecessor than is the case in the Vipers.

It is, I think, a legitimate inference that the cobra, having lost one poison-fang, would remain unarmed for a longer period than a viperine snake, in which latter the new tooth is able to get into place and be ready to be fixed before the loss of its predecessor. May this not explain the preference shown by the Indian jugglers† for the

* Dr. Weir Mitchell ("On the Venom of the Rattlesnake," Smithsonian Contributions, 1861) had become aware that the succession was regular, and that the new tooth came up by the side of the old one; he did not, however, arrive at a correct interpretation of the positions and movements of the successional teeth as they are developed and rise into place.

† Snake-charmers do, however, sometimes make use of viperine snakes, *e. g.* the Tic Polonga (*Daboia Russellii*).

cobra as a snake for snake-charming exhibitions? A cobra deprived of its poison-fangs would remain harmless for some little time, but a rattlesnake similarly disarmed would sooner replace its lost weapon.

The colubrine poisonous snakes are less specialized than those of the viperine type; the maxillary bones are immovable, and are not very short; they also often carry a few other teeth behind the poison-fang. It is interesting to see that this lower degree of specialization is found in the processes of development and succession, so that the region in which the successional poison-fangs are being formed is strikingly similar to that in which the ordinary ophidian teeth are developed, whilst in the viperine snakes it is strikingly dissimilar and highly specialized.

To return to the consideration of the tooth-forming region of the vipers. I have shown that the teeth are developed in two parallel series, separated by a connective-tissue partition, which is prolonged so as to hang as a free fold (*b* in figs. 1 & 2) into the pouch occupied by the working tooth, and that the new tooth is taken from the one or the other series alternately. The successional teeth are arranged in two straight lines in the rattlesnake (fig. 2) and in two curved lines in the viper (fig. 1); but at another point in the rattlesnake's head the lower successional teeth are arranged along a slight curve, so that this difference is not of any moment.

The appearances presented by the tooth-forming area differ according as the section is taken near to the base or near to the tip of the working tooth. Close to the maxillary bone we see either the bases of two teeth, as in fig. 4, or the base of one tooth and the vacant space just vacated by another, as would be seen if we had a section at the base of the teeth represented in fig. 2. A little further down we have the state of things represented in fig. 3 (also from the same viper as figs. 1 & 4), in which the bases of four teeth are seen, which may be identified and compared with those in the other figures by their numbers, whilst as we approach nearer to the tip of the working tooth as many as ten teeth come into view.

Nearer to the tip of the active tooth we have passed beyond the region where tooth-development is most active, so that figs. 1 & 2 may be taken as giving the best idea of the parts. In order to make the relations of the several teeth to one another clear, I have constructed the diagram fig. 12 (p. 382), which is intended to show the positions of the transverse sections which have been figured on Plate 37; an actual drawing of a longitudinal section would not have answered the purpose so well, as the several teeth are so close together as to appear confused.

It now remains to give a short account of the structure and development of the individual teeth, and of the manner in which they become attached. The earliest tooth-germ is not distinguishable from that of any other tooth. A band of epithelium, which may be seen at *f* in figs. 1 & 10, grows out into the connective tissue beyond the youngest germ; its extremity becomes converted into an extinguisher-like enamel-organ covering over a newly forming dentine pulp. A transverse section of such a young germ is shown in fig. 6, and at $_8$ and $_9$ in fig. 2. The dentine pulp is surrounded by a thin

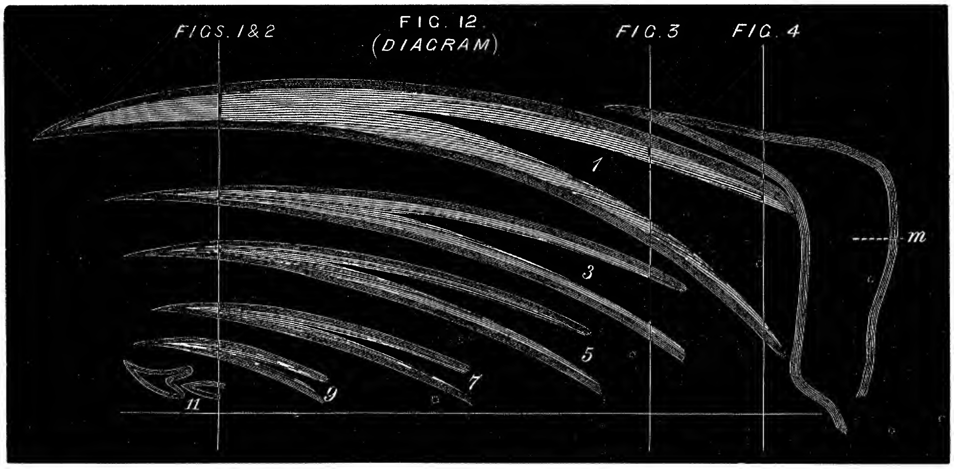


Fig. 12.—A diagram constructed from a comparison of many longitudinal sections. An inspection of this serves to explain why figs. 1 & 2 show in transverse section as many as ten teeth, while sections nearer the base, *e. g.* figs. 3 & 4, show but four and two teeth respectively.

layer of formed dentine, and outside this comes a continuous layer of enamel-cells (internal epithelium of the enamel-organ). A little later on, as the tooth-germ elongates, a shallow depression appears on the one side (fig. 8) into which the layer of enamel-cells runs without break; the groove deepens, but at first the enamel-cells do not undergo any modification (see fig. 7) in that groove which is to become the canal for the conveyance of the poison.

But at a later stage, when the crescentic pulp, with its layer of formed dentine around it, has arched round so that its extremities are approximating (fig. 9), a most remarkable change has taken place in that part of the enamel-organ which lines the groove. No distinct layer of enamel-cells can any longer be traced, but the whole space included in the concavity of the crescent is occupied by a mass of branched cells, which in their general aspect strongly recall the stellate tissue or reticulum which forms so large a part of mammalian enamel-organs. And as it is beyond all question that the enamel-organ, destined to play no active part in this concavity or canal, has become transformed into a sort of stellate tissue, are we to regard the stellate tissue of a mammalian enamel-organ as a retrograde metamorphosis of a superfluous tissue? Before becoming acquainted with the enamel-organ of a poison-fang I was aware, and had expressed an opinion, that the stellate tissue was quite non-essential, for there are many enamel-organs which form enamel of perfect structure and appreciable thickness which have never possessed any parts save their external and internal epithelium.

Ultimately this stellate tissue seems to wither up and leave the canal empty, so that we must regard it, in this place at all events, as a step on the way towards the disappearance of the enamel-cells; and as it is hardly to be found in advance of the thin edge of calcified dentine, it does little more than fill a void. A thin layer of enamel is formed round the exterior of a poison-fang; but after what has been said, I need hardly say that no enamel lines the interior of the poison-canal.

There is nothing noteworthy about the dentinal pulps of poison-fangs; but their manner of attachment to the bone merits a word or two of notice.

Looking with the naked eye at the bone which carries the poison-fangs, to which they are anchylosed by their bases, there is seen to be a sort of hood or parapet of bone rising up in front of the fangs. This would appear to add to their strength, as the tendency of the blow struck by the snake would be to displace the tooth forwards. This parapet of bone is seen in section in fig. 4 and fig. 3 (*m*). The firm attachment of the tooth is likewise secured by the form of its own base, which is convoluted (see figs. 4 & 5) and recalls the structure of labyrinthodont teeth at that point in the crown where their complexity of structure first commences; this convolution of the dentine at the base of a tooth which is attached by anchylosis is quite common in the teeth of both fishes and reptiles. The dentine interdigitates with the supporting bone, the line of junction consisting of a cloudy opaque calcified tissue, in which, without the use of acids, no definite structure can be seen. Immediately outside this there is very coarse bone, with very large irregular lacunæ, which gradually merges into the regular fine-textured bone of the snake's jaw.

When the new tooth is about to become attached, a sort of network or scaffolding of new bone is thrown out, which meets and interdigitates with the convoluted dentine, which is being simultaneously calcified. This new bone, coarse in texture and very rapidly developed, springs up outside the tooth-sac, and takes its origin from the surface of the old bone; it constitutes that "bone of attachment" to which I have elsewhere called attention as being invariably present where a tooth becomes fixed in place by the process of anchylosis. This "bone of attachment," present in large quantity both in the cobra and in viperine snakes, is specially developed for every tooth, and is removed when the tooth is shed, a fresh scaffolding being put forth for its successor.

The duct of the poison-gland was formerly supposed to become enclosed within the tube of the poison-fang by the process of the latter growing around it. This, however, does not happen; for that part of the tooth in which the groove has its lips closed, so as to form a tube, is completed before the tooth moves into place upon the maxillary bone.

That portion which is not thus completed is very short, and is impressed by an open groove only. Moreover the new tooth comes by the side of the old one, and does not occupy the same spot, so that such an arrangement would be all but impossible.

The poison-duct opens close above the base of the tooth, where the groove in which the upper end of the poison-tube terminates is situated. The close apposition of the hood of mucous membrane which covers the poison-fangs in secures a large proportion of the poison passing down it, but no more absolute communication than this takes place. In longitudinal section the remnant of the enamel-organ within the tube has a superficial resemblance to a duct within the tooth, and by this I was at first deceived. Examination of specimens in more perfect preservation, however, has rendered me certain that no sort of duct with soft walls exists within any part of the tube in the poison-fang.

Description of the Plate.

PLATE 37.

The same lettering applies to all the figures.

1. The poison-fang at present in use.
2. The tooth which stands next in order to replace the one in use.
3. The third in order of succession, &c.

a. Epithelium of the mouth.

a'. Epithelium continued into the pouch.

b. Connective-tissue septum, which serves to keep to their respective sides the teeth of the two parallel series when they move into position.

c. Section of pouch of mucous membrane which covers in the poison-fangs whilst recumbent.

d. Formed dentine.

e. Enamel-cells of the enamel-organ.

e'. Enamel-cells in the groove which is to become the canal for the conveyance of the poison.

f. Process of epithelium passing beyond the youngest tooth-germ, from which the next enamel-organ will be formed.

g. Band of epithelium connecting the tooth-germs with the epithelium of the surface.

h. Space in which the poison-fang lies whilst at rest.

k. Coarse "bone of attachment."

m. Maxillary bone.

n. Transverse bone.

p. Dentinal pulp.

Fig. 1. From English viper.

Transverse section of poison-fang and its nine successors. The tooth in use (1) is on the point of being replaced by a successor (2), which has already passed from the region in which it was developed into the cavity of the pouch. Between the two lies the connective-tissue flap, which helps to guide it into place, to keep it to its own side, and to keep it straight. Beneath these two teeth are eight successors arranged in pairs in two parallel series, the new tooth being taken alternately from either side.

On the right (*f*) is a process of epithelium from which a new enamel-germ would be formed; the corresponding epithelial process of the left-hand series of teeth is not clearly visible.

The position of this and some of the other sections will be better understood by a reference to the woodcut, fig. 12 (p. 382).

Fig. 2. From a full-grown rattlesnake.

A section in most respects similar to fig. 1, with the exception that the tooth in use (1) is not to be replaced so speedily as the corresponding tooth in fig. 1. The partition (*b*) is deflected to one side, there being only one tooth free in the pouch.

Fig. 3. English viper.

This section is taken from the same specimen as fig. 1, but through a spot nearer to the fixed base of the tooth (see Diagram, fig. 12, p. 382).

At the top of the figure is seen in section the parapet of bone which stretches up from the body of the maxillary bone in front of the teeth.

2, 3, 4. Portions of three successional tooth-germs occupying the remaining space between the parapet of the maxillary and the transverse bone.

Fig. 4. English viper.

From the same specimen as figs. 1 & 3; taken through the attached base of the poison-fang (1).

It is to be noticed that there is room for two poison-fangs, side by side, and that these two positions are alternately occupied by the working teeth.

The tooth 2, which is rapidly becoming attached, will be fixed in place by a framework of coarse bone (*k*), which shoots out from the maxillary bone and becomes united with the dentine.

Fig. 5. Indian cobra.

Transverse section, immediately behind the poison-fang.

The successional teeth come to occupy the same spot as their predecessors, and are developed, unlike those of viperine snakes, in a single series.

Compare this figure with that of the successional teeth of a harmless snake (Phil. Trans. part i. 1875).

Fig. 6. Transverse section of a very young tooth-germ from an English viper.

It does not differ as yet in any particular from the tooth-germ of any other Ophidian tooth.

Fig. 7. Viper. Tooth-germ a little older.

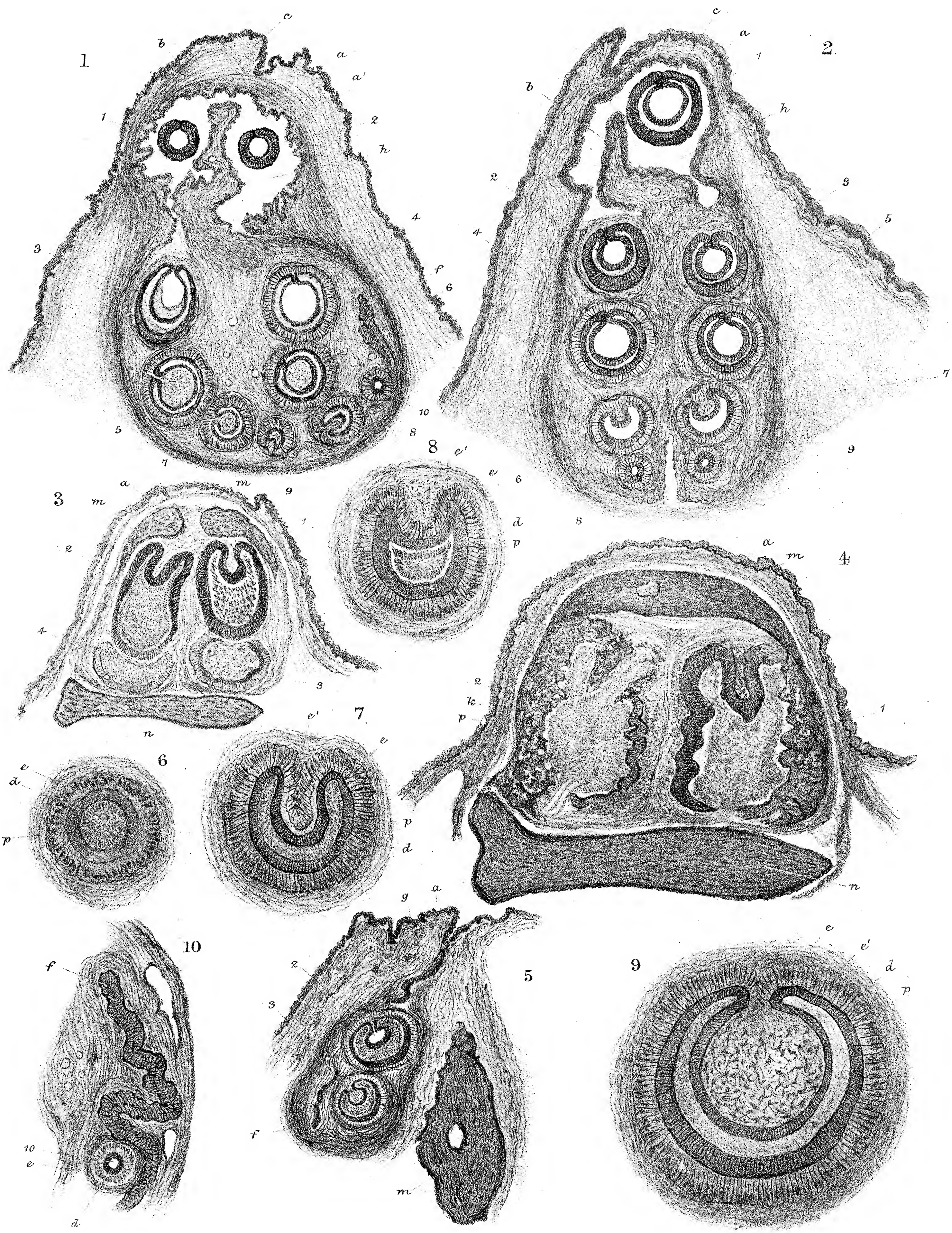
The groove, to become afterwards a canal, has commenced, but as yet the enamel-organ occupying it is not altered from that surrounding the rest of the tooth.

Fig. 8. English viper, at a somewhat later stage.

Fig. 9. English viper, later stage.

The enamel-organ occupying the interior canal has become transformed into a tissue of stellate cells (e').

Fig. 10. Process of epithelium, *f* (enamel-germ of KÖLLIKER), from which a yet younger enamel-organ will ultimately be formed; at *e*, *d* is seen the youngest tooth-germ as yet actually formed.



C. S. Tomes del^t. W. West & Co. lith.